

REVISION OF THE DASYURID MARSUPIAL GENUS *ANTECHINOMYS* KREFFT

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ABSTRACT

Antechinomys is regarded as a monotypic genus containing only *A. laniger* Gould, 1856, which is represented by two distinctive allopatric forms, the nominate form and the 'spenceri' form. The 'spenceri' form differs from the nominate form in its lower nipple number, larger size, and relatively more arid habitat.

It is suggested that *Antechinomys* is at present actively speciating with clines developing between central, relatively more arid regions and the dry but less arid, peripheral, regions of Australia. The differences interpreted here as clinal were formerly regarded as indicators of full specific status for *spenceri* Thomas, 1906.

The closest affinities of *Antechinomys* are clearly with species of *Sminthopsis*, and in particular, *S. crassicaudata*.

The incidence and origin of monotypic marsupial genera in Australia is considered and it is suggested that *Antechinomys* evolved in middle to late Tertiary times in response to the development of widespread relatively arid regions in Australia.

The generic status of *Antechinomys* has not been questioned since 1867 when Krefft proposed the generic name for the species *laniger* Gould, 1856. However, the number of species in the genus has been in doubt. Lidicker and Marlow (1970, p. 216) in their excellent review state in regard to a specimen (BM No. 1939.2997) noted by Tate (1947, p. 125) from Cedar Bay, north Queensland, that this '... disjunct population, if it still survives, may very well represent a separate taxon ...'. Similarly Parker (1973, p. 8) suggests that the north Queensland specimen and specimens from northeastern Northern Territory could represent an undescribed taxon.

Catalogue numbers referred to are abbreviated as follows: BM, British Museum (Natural History); C, National Museum of Victoria; J or JM, Queensland Museum; NTM, Northern Territory Museum (collections in the Arid Zone Research Centre, Alice Springs); SAM, South Australian Museum; WAM, Western Australian Museum; B, Butler collection, Western Australian Museum; 72.3.497 (for example), fossil vertebrate collection, Western Australian Museum.

Measurements have been made only on adults. Points from which cranial measurements have been made are shown in Fig. 1. Tail length as described by Thomas (1888) and appropriate for marsupials has been measured from the vent to the tail tip. This

practice is not universally followed (e.g. Lidicker and Marlow 1970). Condylbasilar length is taken from the posterior edge of the occipital condyles to the posterior edge of the I¹ alveolus. Zygomatic width is not equivalent to Lidicker and Marlow's cranial breadth. Bullar length of Lidicker and Marlow is said by them (p. 214) to be the 'Anterior-posterior length including both alisphenoid and petrotic portions of bullae ...'. Measurements given by them for bullar length of Warburton Range animals indicate that they also involve the inflated portion of the paroccipital process. The same structures are included in bullar length of the present study.

Dental terminology is that used by Archer (1976a). Cranial terminology is shown in Fig. 1 (and follows Archer 1976b). Modern species names are those used by Ride (1970), Laurie and Hill (1954) and Archer (1975).

Family DASYURIDAE Genus *Antechinomys* Krefft, 1866

TYPE SPECIES: *Antechinomys laniger* Gould, 1856
(by monotypy).

GENERIC DIAGNOSIS

Small dasyurids similar to *Sminthopsis* but differ from these in that hallux of hind foot absent; limbs

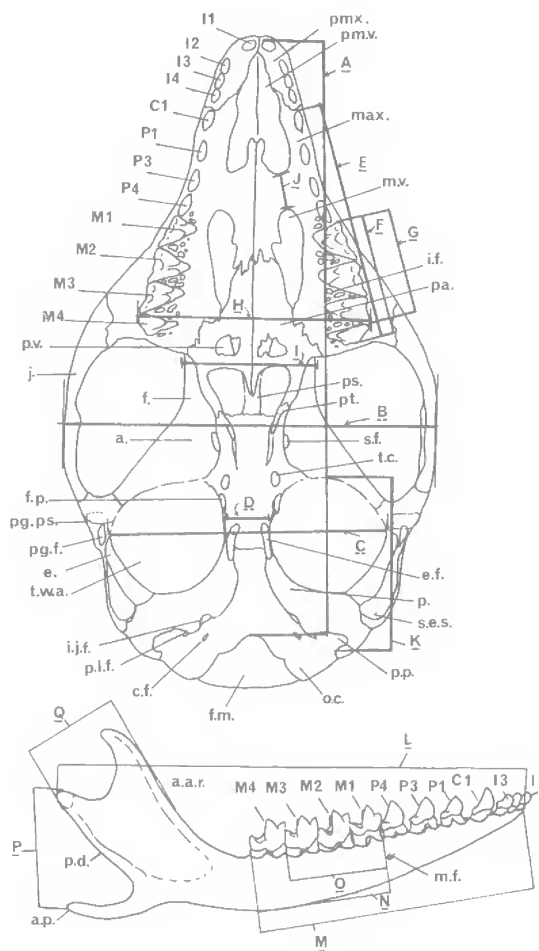


FIG. 1: Terminology and mensuration of skull and dentary of *Antechinomys* (based on the 'spenceri' form of *A. laniger*). *a.*, alisphenoid; *a.a.r.*, anterior border of ascending ramus; *a.p.*, angular process; *c.f.*, condylar (and/or hypoglossal) foramen; *e.*, ectotympanic; *e.f.*, entocarotid foramen; *f.*, frontal; *f.m.*, foramen magnum; *f.p.*, foramen pseudovalve; *i.f.*, interdental fenestrae; *i.j.f.*, foramen of internal jugular canal; *j.*, jugal; *max.*, maxilla; *m.f.*, mental foramen; *m.v.*, maxillary vacuity; *o.c.*, occipital condyle; *p.*, periotic; *pa.*, palatine; *p.d.*, posterior border of dentary; *pg.f.*, postglenoid foramen; *pg.ps.*, postglenoid process; *p.l.f.*, postero-lateral foramen; *pm.v.*, premaxillary vacuity; *pmx.*, premaxilla; *p.p.*, paroccipital process; *ps.*, pre-sphenoid; *pt.*, pterygoid; *p.v.*, palatine vacuity; *s.e.s.*, squamosal epitympanic sinus; *s.f.*, sphenorbital fissure; *t.c.*, transverse canal; *t.w.a.*, tympanic wing of alisphenoid. *A-Q*, measurements and positions from which they were made. *A*, basicranial length (BL, Table 1); *B*, zygomatic width (ZW); *C*, maximum bullar width (OBW); *D*, minimum bullar width (IBW); *E*, C^1-M^4 ; *F*, M^1-M^4 ; *G*, M^1-M^3 ; *H*, $R-LM^3$; *I*, minimum interorbital width (IO); *J*, inter-palatal vacuity distance (IPVD); *K*,

relatively longer; and tail with well-developed distal brush. Differ from all other dasyurids by combination of following characters: squamosal-frontal contact on outside of braincase; nasals not widened posteriorly; palatine vacuities present; tail thin; hind foot narrow, elongate, with interdigital pads fused into single trilobed pad and lacking post-interdigital pads; very small to absent entoconids; no posterior cingulum on upper molars; P_4 completely unreduced; C_1 premolariform.

GENERIC DISCUSSION

Tate (1947, p. 125) notes that *Antechinomys* '... seems to be derived from the same ancestry as *Sminthopsis*, and from that section of *Sminthopsis* to which *S. crassicaudata* belongs ...'. Additional reasons for regarding *Antechinomys* and *Sminthopsis* to share a common ancestor, include the fact that in both, the squamosal and frontal bones contact on the outside of the cranium, thereby excluding the more normal dasyurid alisphenoid-parietal contact. The structure of the *Antechinomys* talonid also reveals affinity to *Sminthopsis* and particularly *S. crassicaudata*, in that there is an approximation of the entoconid to the lingual end of the hypocristid. Of the two commonly recognized forms of the genus *Antechinomys*, the nominate form is least specialized and hence regarded as structurally ancestral, and it is this form which shows the closest resemblance to *Sminthopsis crassicaudata*.

Antechinomys is considered in the present study to be monotypic. As such, it is one of 30 such marsupial and monotreme genera in New Guinea and Australia (based on reviews by Ride 1970 and Laurie and Hill 1954). Several of these such as *Myrmecobius*, *Thylacinus* and *Notoryctes* are also highly specialized forms in that they do not resemble structurally ancestral marsupials in the supra-familial groups to which they belong. Other monotypic genera such as *Antechinomys*, *Dasyercus*, *Dasyuroides* and *Sarcophilus* are less highly specialized, and structurally similar genera (*Sminthopsis*, *Antechinus* and *Dasyurus* respectively) may be found in the family groups to which they belong. These two sorts of monotypic genera may have had different origins. The fossil history of all these monotypic genera is poorly known, but what is known suggests that, with the

bullar length (includes paroccipital process or paroccipital tympanic wing if developed) (Bul); *L*, dentary length (DL); *M*, I_1-M_4 ; *N*, M_1-M_4 ; *O*, M_1-M_3 ; *P*, tip of angular process to articular condyle (C-AP); *Q*, articular condyle to anterior border of ascending ramus (C-AR).

possible exception of *Wallabia*, none has been represented in the past by more than one species at any given time. In the case of the highly specialized forms such as *Myrmecobius*, *Thylacinus* and *Notoryctes*, this seems surprising. These animals are presumably specialized in response to their occupation of unique ecological niches. If they have had a relatively long history to specialize, why have they not also speciated within these unique niches? Why is there only one species of *Myrmecobius* or *Tarsipes* when there are many types of termites and blossoms throughout Australia? In several similar and possibly related lineages elsewhere in the world, speciation has taken place. South American marsupial borhyaenids are structurally very similar to *Thylacinus*, yet at any one time, there were at least two or three genera of borhyaenids. All of these differed from each other at least in size and tooth shape, presumably having adapted to different diets. The origin of the less highly specialized monotypic genera such as *Dasyercus*, *Dasyuroides*, *Caloprymnus* and *Chaeropus* may be late Cainozoic climatic change and the relatively recent production of extensive areas of arid lands in central Australia. These forms may only now be speciating, and it seems likely that *Antechinomys* is a monotypic genus of this sort.

Antechinomys laniger (Gould)

(Figs. 1–2, Plates 8–13)

Phascogale lanigera Gould, 1856, Letterpress for Plate 33.

Antechinomys spenceri Thomas, 1906, p. 331.

TYPES

Phascogale lanigera Gould, 1856.

HOLOTYPE: BM 47.8.14.22 (skin) and 47.12.4.5 (skull), adult male, collected by Sir Thomas Mitchell.

TYPE LOCALITY: Gould (1856, letterpress to plate 33) '... discovered by Sir Thomas Mitchell, during one of his expeditions into the interior of Australia'. Thomas (1888, p. 310)—'New South Wales.'. Tate (1947, p. 125)—'... on the plains between the Murray and Darling Rivers in New South Wales.'.

Antechinomys spenceri Thomas, 1906.

HOLOTYPE: BM 97.11.3.12, skull and carcase in alcohol, obtained by Mr P. Byrne (Spencer 1896, p. 42). Evidently not collected by Spencer on the Horn Expedition as claimed by Thomas 1906, p. 331.

TYPE LOCALITY: Thomas (1906, p. 331)—'Hab. Charlotte Waters, Central Australia.'. Spencer (1896, p. 40) only mentions specimens coming from '... Missionary Plains in the Finke Valley, between the James Range to the south and the McDonnell Ranges to the north.', collected by the Horn Expedition. He gives no locality for additional specimens obtained by Mr P. Byrne (p. 42).

Latter specimens included the only two females obtained (Spencer 1896, p. 42). Holotype must be one of these two females obtained by Mr P. Byrne because Thomas (1906, p. 332) says holotype is one of the specimens referred to by Spencer (1896).

DIAGNOSIS

The species diagnosis is the same as that for the genus until additional species are known.

DESCRIPTION

TAIL: Tail invariably thin. Brush length absolutely longer in 'spenceri' form, but proportionately similar in all populations except Lake Grace where brush is proportionately larger. Tail-vent length exceeds head-body length.

EAR: Ear length in all individuals large, but shorter in nominate than 'spenceri' form.

HIND FOOT: interdigital pads fused as single granular trilobed pad. Toe pads smooth, not granular. Hind foot narrow. Hallux absent. Ventral surface covered by fine hairs, including interdigital pad.

PELAGE MARKINGS: Dark ring around eye. Mystacial vibrissae area of face dark. Middle of forehead with dark patch. Crest of tail dark.

NIPPLE NUMBER: Four, six, eight and ten nipples have been recorded, the latter probably being abnormal. Lidicker and Marlow regard number as distinctive of allopatric forms, 'spenceri' having six and the nominate form eight.

POUCH: Varies in morphology and size with reproductive condition. Woolley (1974) and Lidicker and Marlow (p. 219) review various conditions of pouch.

CRANIUM AND DENTARY: Cranium narrow, and more so in the nominate than 'spenceri' form. Rostrum narrow and elongate. Antero-dorsal part of each frontal convex producing in this area narrow antero-posterior depression in midline of skull. No postorbital processes. Lacrimal bone has wide lateral flanges that extend back over anterodorsal rim of orbit. Commonly lacrimal bones also have posterodorsal flanges. Posterodorsal area of maxilla inflated laterally with development of sinuses. Infraorbital foramen large and commonly perforated ventrally by roots of upper molars. Lacrimal foramina single and on or posterior to rim of orbit. Alisphenoid and periotic tympanic wings variously enlarged. Paroccipital tympanic wing variously inflated to uninflated. All tympanic wings absolutely and proportionately larger in

TABLE 1: ABSOLUTE MEASUREMENTS IN *Antechinomys*.

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
<i>Antechinomys laniger</i> (total modern)						A. l., Tobermory					
BL	27	24.4 \pm .29	21.7-27.1	1.53	6.26	6	23.2 \pm .79	21.7-26.9	1.93	8.34	
ZW	30	14.5 \pm .15	12.9-16.0	0.85	5.84	6	14.1 \pm .47	12.9-16.0	1.16	8.21	
OBW	31	10.4 \pm .14	9.0-11.6	0.77	7.40	6	9.8 \pm .41	9.0-11.6	1.01	10.34	
IBW	30	2.4 \pm .06	1.8- 3.3	0.34	14.28	6	2.4 \pm .11	2.1- 2.7	0.27	11.18	
C ¹ -M ⁴	32	10.2 \pm .10	9.2-11.4	0.58	5.65	6	9.8 \pm .33	9.2-11.4	0.80	8.14	
M ¹⁻⁴	33	5.3 \pm .10	4.6- 5.7	0.26	4.85	6	5.1 \pm .13	4.8- 5.7	0.31	6.07	
M ¹⁻³	37	4.7 \pm .04	4.0- 5.3	0.23	4.77	8	4.6 \pm .06	4.3- 4.8	0.17	3.67	
R-LM ³	31	8.4 \pm .10	7.5- 9.6	0.53	6.31	6	8.1 \pm .32	7.5- 9.6	0.77	9.53	
IO	30	5.5 \pm .06	4.9- 6.0	0.35	6.31	6	5.2 \pm .11	4.9- 5.7	0.27	5.16	
IPVD	31	2.2 \pm .07	1.4- 3.0	0.37	16.61	6	2.0 \pm .10	1.8- 2.4	0.22	11.18	
DL	33	19.7 \pm .20	18.3-21.9	1.13	5.74	6	18.7 \pm .70	17.4-21.9	1.72	9.18	
I ₁ -M ₄	33	11.9 \pm .10	10.8-13.5	0.59	4.88	6	11.8 \pm .33	10.8-13.5	0.82	6.94	
M ₁₋₄	36	6.1 \pm .05	5.3- 6.5	0.29	4.76	6	5.9 \pm .15	5.6- 6.6	0.37	6.25	
M ₁₋₃	38	4.5 \pm .04	3.9- 4.9	0.22	4.91	8	4.4 \pm .08	4.2- 4.9	0.23	5.29	
C-AP	31	6.0 \pm .10	5.3- 6.9	0.55	9.15	6	5.7 \pm .25	4.9- 6.9	0.60	10.55	
C-AR	32	3.6 \pm .05	3.2- 4.2	0.28	7.89	6	3.6 \pm .16	3.2- 4.2	0.39	10.76	
A. l., Roper River						A. l., Nullarbor (subfossil)					
BL	3	23.8 \pm .15	23.5-24.0	0.25	1.07	8	10.0 \pm .13	9.3-10.4	0.37	3.72	
ZW	3	14.2 \pm .17	13.9-14.5	0.30	2.11	11	5.2 \pm .06	4.9- 5.5	0.18	3.54	
OBW	3	10.0 \pm .09	9.8-10.1	0.16	1.58	10	4.6 \pm .05	4.3- 4.8	0.17	3.77	
IBW	3	2.9 \pm .06	2.8- 3.0	0.10	3.45	-	-	-	-	-	
C ¹ -M ⁴	3	10.0 \pm .06	9.9-10.1	0.10	1.00	-	-	-	-	-	
M ¹⁻⁴	3	5.2 \pm .06	5.1- 5.3	0.10	1.92	9	2.7 \pm .14	2.0- 3.3	0.42	15.54	
M ¹⁻³	3	4.6 \pm .04	4.5- 4.7	0.07	1.52	31	19.1 \pm .09	18.0-20.2	0.52	2.72	
R-LM ³	3	8.2 \pm .04	8.1- 8.2	0.07	0.85	39	11.2 \pm .04	10.7-11.7	0.25	2.20	
IO	3	5.1 \pm .06	5.0- 5.2	0.10	1.96	37	5.9 \pm .03	5.7- 6.4	0.16	2.79	
IPVD	3	2.5 \pm .25	2.1- 2.7	0.42	16.98	37	4.5 \pm .02	4.2- 4.8	0.15	3.31	
DL	3	19.5 \pm .32	18.9-20.0	0.55	2.83	24	5.7 \pm .04	5.3- 6.0	0.21	3.75	
I ₁ -M ₄	3	11.6 \pm .15	11.3-11.8	0.25	2.20	33	3.7 \pm .04	3.2- 4.3	0.24	6.37	
M ₁₋₄	3	6.0 \pm .06	5.9- 6.1	0.10	1.67						
M ₁₋₃	3	4.5 \pm .12	4.3- 4.7	0.20	4.44						
C-AP	3	5.6 \pm .06	5.5- 5.7	0.10	1.79						
C-AR	3	3.6 \pm .06	3.5- 3.7	0.10	2.78						
A. l., Warburton Range						A. l., Lake Grace					
BL	8	25.2 \pm .21	23.0-26.0	0.59	2.36	2	24.8 \pm .22	24.6-24.9	0.32	1.28	
ZW	9	14.7 \pm .17	14.1-15.6	0.50	3.40	2	14.8 \pm .00	14.8-14.8	0.00	0.00	
OBW	9	11.0 \pm .12	10.5-11.5	0.38	3.42	2	10.0 \pm .00	10.0-10.0	0.00	0.00	
IBW	9	2.1 \pm .06	1.8- 2.3	0.17	8.07	2	3.3 \pm .00	3.3- 3.3	0.00	0.00	
C ¹ -M ⁴	9	10.5 \pm .13	10.1-11.1	0.39	3.67	2	10.5 \pm .16	10.3-10.6	0.22	2.13	
M ¹⁻⁴	9	5.4 \pm .05	5.1- 5.6	0.16	3.00	2	5.5 \pm .07	5.4- 5.5	0.10	1.82	
M ¹⁻³	10	4.8 \pm .04	4.7- 5.0	0.12	2.59	2	4.8 \pm .00	4.8- 4.8	0.00	0.00	
R-LM ³	9	8.8 \pm .08	8.4- 9.0	0.25	2.90	2	8.7 \pm .00	8.7- 8.7	0.00	0.00	
IO	8	5.8 \pm .05	5.7- 6.0	0.13	2.25	2	5.8 \pm .07	5.7- 5.8	0.10	1.72	
IPVD	9	2.4 \pm .10	2.0- 2.9	0.30	12.41	1	2.7 \pm .00	2.7- 2.7	0.00	0.00	
DL	9	20.1 \pm .19	19.3-20.9	0.58	2.88	2	19.9 \pm .43	19.2-20.6	0.86	4.32	
I ₁ -M ₄	9	12.1 \pm .11	11.7-12.8	0.33	2.69	2	12.3 \pm .20	12.1-12.5	0.28	2.30	
M ₁₋₄	9	6.2 \pm .06	5.7- 6.5	0.19	3.12	2	6.2 \pm .00	6.2- 6.2	0.00	0.00	
M ₁₋₃	10	4.5 \pm .05	4.2- 4.7	0.15	3.31	2	4.6 \pm .07	4.5- 4.6	0.10	2.17	
C-AP	8	6.5 \pm .08	6.2- 6.7	0.22	3.44	1	5.6 \pm .00	5.6- 5.6	0.00	0.00	
C-AR	9	3.7 \pm .06	3.2- 4.0	0.17	4.48	1	3.3 \pm .00	3.3- 3.3	0.00	0.00	

'spenceri' than nominate form. Ectotympanic variably enclosed by alisphenoid tympanic wing. Sphenorbital foramen separated from foramen rotundum by variously wide bar of alisphenoid. Foramen rotundum larger than transverse canal and entocarotid foramina. Entocarotid canal variably developed, being often complete enough to obscure ventral view into cranium in 'spenceri' form, while leaving broad direct ventral opening into cranium in nominate form. Transverse canal large but variously wide depending on development of tympanic wings.

Foramen pseudovale varies in width and length, being narrow in 'spenceri' form and wider in nominate form. Internal jugular canal formed between periotic and basioccipital has near vertical mesial wall in 'spenceri' form, less vertical wall in nominate form. Basioccipital keeled antero-ventrally in midline. In some specimens (e.g. WAM M2368) periotic has small bony process which extends antero-mesially across posterior lacerate foramen towards internal jugular canal foramen. Pterygoid or hamular process, when complete, generally has tuberosity, or expanded tip at distal end. Palatal spine well-developed when complete, being almost as long as hamular process of pterygoid. All palatal vacuities very large in length and width. Inter-dental fenestrae numerous and palate between consecutive molars commonly reduced to lattice of bony trabeculae. Externally, squamosal contacts frontal excluding parietal-alisphenoid contact. Nuchal crest commonly produced between occipital and parietal bones. Occasional interparietal ossifications present.

Dentary distinctive in having almost parallel anterior edge of ascending ramus and posterior edge of dentary. Articular condyle high and much closer to tip of ascending ramus than tip of angular process. Dentary slender and very shallow at anterior end. Symphysis short, back to level of P_3 in adult, and unfused (contrary to suggestion of Tate 1947, p. 125).

DENTITION: I^1 just taller-crowned than I^4 , subequal to I^3 , and larger than I^2 . I^4 crown larger than I^3 crown which is subequal to I^2 crown. I^{2-4} with extremely reduced to absent posterior cusps. I^1 and I^2 and I^4 and C^1 separated by diastemata. C^1 premolariform with (in unworn state) distinct

anterior and posterior cingular cusps. C^1 subequal to or just larger in crown height and length to P^1 , but subequal to or smaller than P^3 , and conspicuously smaller than P^4 . C^1 without buccal and lingual cingula. P^1 with anterior and posterior cingular cusps and no buccal cingulum. Lingual cingulum variably developed from very reduced to absent. P^3 with anterior and posterior cingular cusps. P^3 frequently has cingulum developed around tooth except just beneath lingual and buccal position of paracone tip. P^1 has small anterior and large posterior cingular cusps. P^4 has small anterior and large posterior cusps. P^4 also have lingual swelling in crown midway along length serving as buttress for paracone. P^4 cingula distributed as in P^3 . DP^4 three-rooted, with six to seven cusps: low protocone, low stA, large stD, variably developed tiny stE, large paracone and large metacone immediately lingual to stD. DP^4 metacrista well-developed. Paracrista absent (presumably result of lack of discrete stB). Pre- and post-protocrista very tiny. All dP^4 cusps sustain wear with age. P^4 slightly taller-crowned than P^3 which is conspicuously larger than P^1 . DP^4 crown as long as P^3 but shorter-crowned than any premolar. M^{1-4} relatively wide, among widest in all dasyurids. Homologue of stA present but indistinguishable from buccal end of anterior cingula M^{1-4} . StA M^1 relatively most distant from stB. StB present M^{1-4} . StD largest M^1 , smallest M^3 . StC absent. StE small and present M^{1-3} either as small cusp or buccal crest connected to posterior flank of stD. Paracone gradient increases from M^1 to M^4 . Metacones M^3 and M^1 subequal in size and smaller than M^2 . Variably present or distinguishable metacone M^4 . Protocones M^1 and M^2 subequal and larger than protocone M^3 which is in turn larger than protocone M^4 . Anterior cingula M^{1-4} confined to antero-buccal corner of tooth and not connected to preprotocrista. No posterior molar cingula. Paracrista increases in size from M^1 to M^4 . Metacristae M^1 and M^3 subequal in length and smaller than metacrista M^2 . Protoconule absent. Metaconule generally absent but sometimes present on M^4 postprotocrista.

I_1 taller-crowned than I_3 which is taller-crowned or subequal to I_2 . I_3 with variably present small posterior lobe generally abutting anterior edge of C_1 . C_1 generally lacks anterior cingular cusp but

Abbreviations: BL, basicranial length; ZW, maximum zygomatic width; OBW, outside bullar width; IBW, inside bullar width; IO, minimum interorbital width; IPVD, inter-palatal vacuity distance; DL, dentary length; C-AP, articular condyle of dentary to tip of angular process; C-AR, C to anterior border of ascending ramus; N, sample number; \bar{X} , sample mean; r , standard error of the mean; OR, observed range; S, standard deviation; CV, coefficient of variation. Locality names abbreviated as follows: Tobermory, N.T.; Roper River, N.T.; Nullarbor, W.A., surface of caves; Warburton Range, W.A.; Lake Grace, W.A.

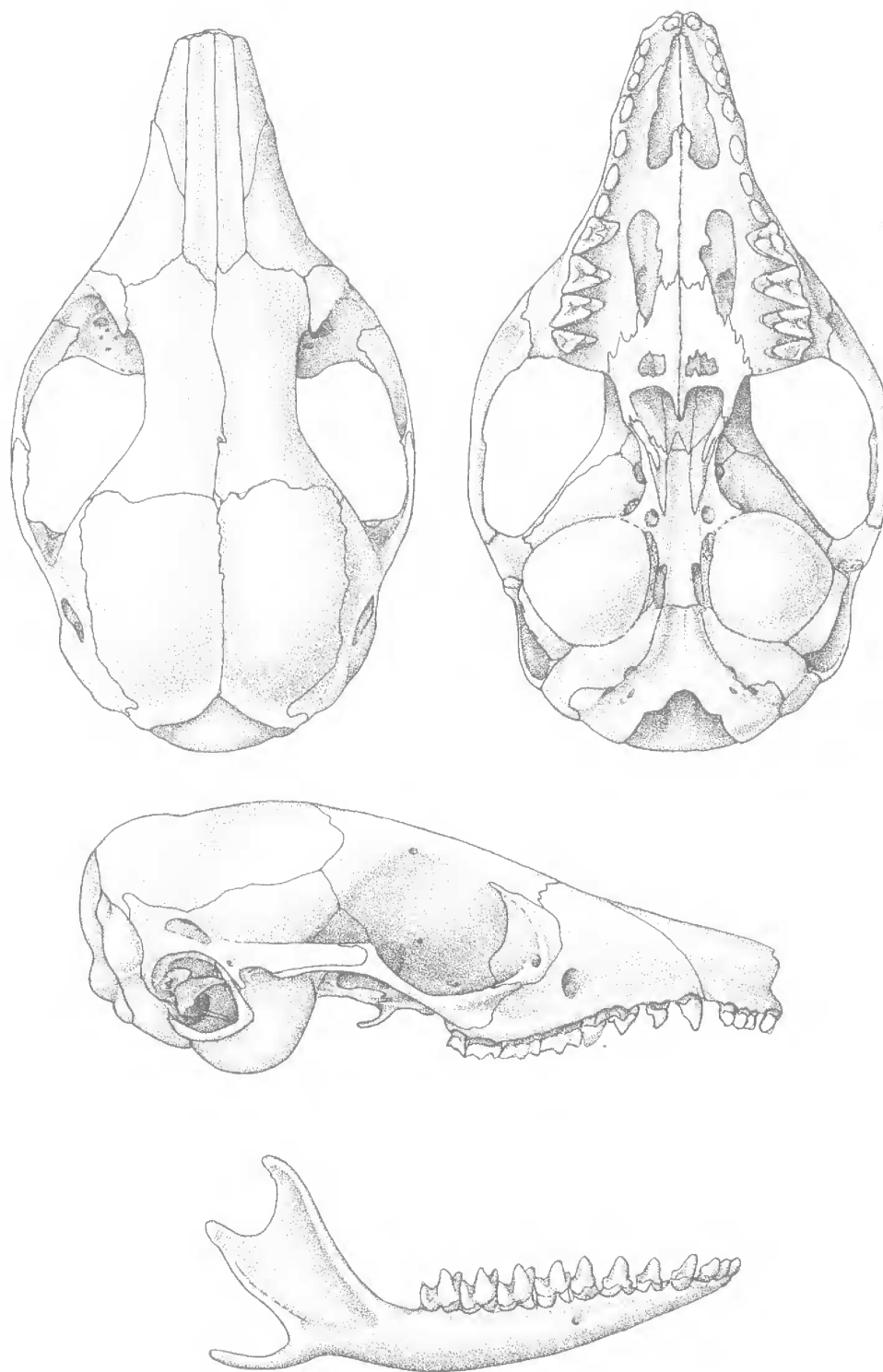


FIG. 2: *Antechinomys laniger* ('spenceri' form). Drawings based on photographs and specimen B1654.

has posterior cingular cusp. C_1 has moderately well-developed buccal and lingual cingula. C_1 crown taller than P_1 crown but shorter than P_3 crown. P_{1-4} generally have small anterior cingular cusps but moderate to large posterior cingular cusps. P_{1-3} have very narrow cingula surrounding crowns. P_4 lacks cingula at base of protoconid. DP_4 has one principal cusp, the protoconid, and one secondary cusp, the hypoconid. DP_4 crown surrounded by narrow cingulum. On posterior flank of protoconid may be miniscule remnant of homologue of metaconid. DP_4 hypoconid connected via posterior hypocristid to postero-lingual cingular cusp possibly representing hypoconulid. Paraconids M_{1-4} increase in size posteriorly. Metaconid and protoconid increase in height posteriorly. Metaconid and protoconid of M_3 subequal to those cusps on M_4 . Hypoconids M_{1-4} subequal in height. Cusps on lingual side of talonid complex. Although normally only an entoconid occurs, in some specimens (e.g. WAM M2860) there are three cusps: small cusp basal to metaconid called here a metastylid; another small cusp, sometimes connected to metastylid by crest, called here an entostylid; and third cusp immediately buccal to entostylid, connected to lingual end of posterior hypocristid, called here the entoconid. Homology of so-called entostylid in doubt and it may in fact be entoconid of other dasyurids. Generally, metastylid M_1 largest and size of cusp decreases posteriorly to M_3 . Generally, size of so-called entostylid smallest M_1 and size increases posteriorly to M_3 . These inverse gradients commonly occur in same specimen (e.g. J23615). Paracristids and metacristids increase in length from M_1 to M_3 . Paracristid and metacristid M_4 subequal to same of M_2 . Trigonid M_1 narrower than talonid. Trigonids and talonids M_{2-3} subequal in width. Talonid M_4 very narrow and high with prominent crest possibly homologous with cristid obliqua of M_{1-3} . Lingual face of cristid obliqua M_4 concave and bounded lingually by basal crest or series of tiny cusps possibly in part homologous with metastylids and entostylids of M_{1-3} .

HABITAT

Lidicker and Marlow describe the habitat in north central N.S.W. and south central Qd of the nominate form as savannah, grass ground cover being interspersed with open areas. Evidently hollow logs and stumps are used as retreats. Troughton (1967) notes that this form is said by Krefft to eat mice in captivity. Parker (1973) notes that animals from the Roper River area apparently inhabit salt-marsh near the river's mouth.

The habitat of the 'spenceri' form is better known. Philpott and Smyth (1967) note the capture of one individual on undulating gibber plain 26 km west of Glengyle Homestead, south-western Queensland. Lidicker and Marlow (p. 227) state that the 'spenceri' form '. . . seems to inhabit a variety of open, tree-less, habitats over much of arid Australia.'. In western Queensland they captured individuals on a sparsely vegetated gravelly plain, in association with *Dasyuroides byrnei* and *Notomys cervinus*. Ride (1970) notes that in the Warburton Range area, Miss P. Robertson found one individual in a burrow. A similar observation was also made by Le Souef and Burrell 1926, who claim the burrows were those of *Notomys*. Ride (1970), regards the instance he notes as unlikely to involve a burrow of a native mouse because the Warburton Range burrow had only one entrance. Another specimen of the 'spenceri' form noted by Ride was captured in a trap-door spider's burrow. Parker (1973, p. 8) notes of these animals in the Northern Territory that they are 'Not uncommon following good seasons, in a variety of country, including sandhills, mulga and gidgea woodland, mitchell grass plains and gibbers'. Finlayson (1961) notes that in 1953-6 the 'spenceri' form was frequently being brought by cats at night into homesteads in the Everard and Musgrave Ranges area of central Australia. Collins (1973) notes aspects of the behaviour of this form in captivity, as does Happold (1972).

Nobody has specifically stated that under normal circumstances individuals of the 'spenceri' form (or the nominate form) have been known to kill small vertebrates for food. On the contrary, Ride (1970, p. 126) says 'The animals which I have kept did not touch meal worms at first, but would eat cockchafer larvae, and large moths and spiders. Lizards placed in a box with them were left untouched.'. Krefft (noted by Troughton 1967) claimed the nominate form, when put into a box with a number of rodents, at once attacked them. This is not necessarily indicative of a normal habit. A *Planigale* will just as readily attack a finger of a hand if it is thrust into a confined space with the frightened animal, but this presumably does not indicate an intention to eat the hand.

REPRODUCTION

Lidicker and Marlow (p. 219) note that a female of the nominate form, taken in late May from El Trune Stn, New South Wales, showed '. . . initial pouch development.'. They also note probable changes in pouch morphology as a function of reproductive condition.

TABLE 2: RATIOS OF CRANIAL, DENTAL, AND EXTERNAL CHARACTERS IN *Antechinus*.

	$\frac{M1-3}{BL}$	$\frac{ZW}{ZW}$	$\frac{BL}{ZW}$	$\frac{IO}{ZW}$	$\frac{M1-3}{R-LM}$	$\frac{M1-4}{C1-M4}$	$\frac{M1-4}{IPVD}$	$\frac{C1-P1}{C1-P1}$	$\frac{C1-P1}{C1-P1}$	$\frac{RL}{RL}$	$\frac{BL}{BL}$	$\frac{CH}{BL}$	$\frac{CH}{CH}$	$\frac{CB}{CH}$	TV	$\frac{HB}{TV}$	Brush	HF	$\frac{Brush}{TV}$	$\frac{M1-4}{M1-4}$
Warb. 10	\bar{X} 4.5	1.73	0.61	0.40	0.55	0.52	0.51	0.50	0.15	2.38	0.35	0.30	0.72	0.43	113*	1.46	54.3	29.7s	0.44	5.4
	O 4.2	1.66	0.58	0.37	0.52	0.47	0.48	0.42	0.05	2.20	0.33	0.28	0.72	0.43	112	(**)	52.8	28.8s	0.44	5.1
	R 4.7	1.80	0.64	0.43	0.58	0.54	0.56	0.62	0.25	2.56	0.37	0.31	0.72	0.43	116		55.8	30.5s	0.44	5.6
W.A. cent. 10	\bar{X} 4.5	1.66	0.54	0.37	0.55	0.51	0.51	0.40	-	-	0.36	0.29	0.71	0.41	101	1.13	-	30.2	-	5.6
	O 4.3	1.58	0.50	0.35	0.51	0.48	0.48	0.30	-	-	(**)	(**)	(**)	(**)	(*)	(**)	-	(*)	-	5.3
	R 4.8	1.70	0.57	0.40	0.61	0.55	0.53	0.47	-	-							-		-	6.0
L.Grace 2	\bar{X} 4.6	1.66	0.45	0.39	0.56	0.52	0.50	0.60	0.13	2.38	0.35	0.24	0.63	0.40	115	1.30	70.1	27.7s	0.62	5.5
	O 4.5	1.66	0.45	0.39	0.55	0.51	0.48	0.56	0.10	2.20	0.33	0.24	0.61	0.38	111	1.26	66.8	25.2s	0.57	5.4
	R 4.7	1.66	0.45	0.39	0.56	0.52	0.51	0.63	0.15	2.55	0.37	0.24	0.64	0.41	118	1.34	73.4	30.2s	0.66	5.5
Tober. 8	\bar{X} 4.4	1.65	0.53	0.38	0.57	0.52	0.50	0.42	0.11	2.18	0.36	0.26	0.65	0.40	108	1.28	48.0	23.7	0.44	5.1
	O 4.2	1.62	0.50	0.35	0.49	0.51	0.48	0.35	0.00	2.00	0.34	0.26	0.60	0.39	101	1.25	39.8	21.0	0.39	4.8
	R 4.9	1.71	0.56	0.39	0.60	0.55	0.53	0.48	0.35	2.60	0.39	0.26	0.70	0.42	113	1.32	55.9	27.0	0.50	5.7
Rop. Riv. 2	\bar{X} 4.4	1.67	0.50	0.36	0.56	0.51	0.51	0.47	0.08	2.15	0.36	0.25	0.65	0.38	110	-	51.0	27.4s	0.43	5.2
	O 4.3	1.66	0.49	0.36	0.55	0.51	0.50	0.46	0.05	2.10	0.35	0.24	0.64	0.38	110	-	47.6	26.3s	0.43	5.1
	R 4.5	1.68	0.50	0.36	0.56	0.51	0.52	0.47	0.10	2.20	0.36	0.25	0.65	0.38	110	-	54.3	28.4s	0.43	5.3
N 59	\bar{X} 4.5	-	-	-	-	0.52	0.53	0.58	-	1.99	-	-	-	-	-	-	-	-	-	5.2
37	O 4.2	-	-	-	-	0.49	0.51	0.43	-	1.80	-	-	-	-	-	-	-	-	-	4.9
	R 4.8	-	-	-	-	0.57	0.57	0.69	-	2.25	-	-	-	-	-	-	-	-	-	5.5
N.S.W.	\bar{X} 4.4	1.69	0.54	0.39	0.57	0.53	0.53	0.42	less	-	0.35	0.25	0.62	0.41	113.5*	1.39	51.8	28.5	0.46	5.1
	O 4.4	1.69	0.54	0.39	0.57	0.53	0.53	0.42	then	-	(**)	(**)	(**)	(**)	103*	(**)	(*)	(*)	(**)	(*)
	R 4.4	1.69	0.54	0.39	0.57	0.53	0.53	0.42	0.20*	-					123*					
N.T. spenc.	\bar{X}	-	-	-	-	-	-	-	-	-	0.32	0.29	0.72	0.41	122.8*	1.49	-	31.6	-	5.6
	O	-	-	-	-	-	-	-	-	-	(**)	(**)	(**)	(**)	103.0*	(**)	-	(*)	-	5.5
	R	-	-	-	-	-	-	-	-	-					143.0*		-		-	5.7
W.Qd spenc.	\bar{X}	-	-	-	-	-	-	-	-	-	0.33	0.27	0.69	0.39	126.4*	1.30	-	30.9	-	5.9
	O	-	-	-	-	-	-	-	-	-	(**)	(**)	(**)	(**)	118.0*	(**)	-	(*)	-	5.6
	R	-	-	-	-	-	-	-	-	-					134.0*		-		-	6.1
Ced. Bay	3.9	-	0.48	0.39	0.50	0.50	0.49	0.63	0.15	2.15	0.38	-	0.65	-	c. 0.96	-	42.5	25.8s	0.45	4.6

Abbreviations: Warb., Warburton Range Mission, W.A.; W.A. cent., all localities in Western Australia except the Warburton Range, Nullarbor, and Lake Grace; L. Grace, Lake Grace, W.A.; Tober., Tobermoray, N.T.; Rop. Riv., Roper River, N.T.; N59, surface of cave (N59) on W.A. Nullarbor; N.S.W., one specimen (WAM 8465) from El Truna Stn, and specimens noted by Lidicker and Marlow (1970); N.T. spenc., 'spenceri' form from N.T. noted by Lidicker and Marlow; W. Qd spenc., 'spenceri' form from Qd noted by Lidicker and Marlow. Ced. Bay, Cedar Bay, N. Qd (BM No. 1939.2997). Number in brackets represents sample size, $C_1-P_1(A)$, space between bases of C_1 and P_1 ; $C_1-P_1(B)$, distance from anterior end of C_1 alveolus to posterior end of P_1 alveolus. RW, rostral width; RL, rostral length; CH, cranial height; Brush, all measured as described by Lidicker and Marlow. Bul, bullar length (see text). CBL, condylobasilar length. TV, tail-vent. HB, nose-vent. HF, hindfoot (su). S indicates standardized measurement as suggested by Lidicker and Marlow. * indicates the figure given by Lidicker and Marlow. ** indicates a ratio obtained by using sample means given by Lidicker and Marlow.

Lidicker and Marlow state that two females of the 'spenceri' form examined from the Warburton Range area had young. WAM M5871, collected 2 November 1963, had three young, and WAM M5886, collected mid-August 1973, had six. Ride (1970) says this form appears to breed in winter. Happold (1972) notes the capture in southwestern Queensland of a female of the 'spenceri' form with pouch young, in late October 1968. Collins (1973) notes a female (locality unspecified) of this form with very small pouch young caught in late October. Two captive individuals (pers. comm. Stanley to Collins) developed pouches in mid-July and by August exhibited behaviour and pouch development indicative of the onset of oestrus. Woolley (1973) notes that birth of the 'spenceri' form is estimated to occur in November. These observations suggest the 'spenceri' form may be monoestrous in apparent contrast to the sympatric species of *Sminthopsis*, *S. crassicaudata* and *S. macroura*.

DISCUSSION OF *Antechinomys laniger*

CONCEPT OF ONE SPECIES IN *Antechinomys*

There is a blurring of characters previously considered (e.g. by Lidicker and Marlow) to be diagnostic of species, in several populations of *Antechinomys*. In particular animals from Tobermoray and the Roper River area of the Northern Territory, from the Nullarbor and Lake Grace area of Western Australia, and Cedar Bay, in Queensland show characteristics which do not clearly enable them to be classified as either *spenceri* or *laniger* in terms of the species concepts employed by Lidicker and Marlow. As a result, two alternative conclusions were considered here: Either the 'aberrant' forms represent yet additional taxa; or they indicate that *spenceri* should be regarded as a form of *A. laniger*, which is a somewhat variable, widespread species. The first alternative seemed the least likely because in at least one population (Tobermoray) morphological and size variation is comparable to that exhibited by *Antechinomys* as a whole. The second alternative seemed more reasonable. Several other dasyurid species have comparable wide geographic ranges of variation such as *Sminthopsis macroura*, *S. crassicaudata*, *Dasyurus cristicauda*, and *Antechinus macedonellensis*. The only particularly unusual areas of distribution for such central Australian wide-ranging species are the Roper River and Cedar Bay localities. However, on morphological grounds, there is no sound basis for distinguishing the Roper River animals from the more central Tobermoray animals. Further, there are suggestions of clines

(some morphological aspects of which are noted by Lidicker and Marlow, p. 223) correlatable with aridity. For example, the Cedar Bay specimen, referred in previous studies to the nominate form, and specimens from the Western Australian Warburton Ranges, referred in previous studies to the 'spenceri' form, are morphologically dissimilar. However, geographically intermediate specimens from Roper River Mission and Tobermoray, Northern Territory, show intermediate conditions. As a result, it has been concluded here that small individuals with small alisphenoid tympanic wings (the nominate form) are distributed geographically around forms which are larger, but which also have relatively large tympanic wings ('spenceri' form), probably because of adaptation to relatively more arid habitats.

CHARACTERS PREVIOUSLY USED TO RECOGNISE MORE THAN ONE SPECIES: Lidicker and Marlow summarize (their table 1) results of their comparisons which lead them to conclude that there are two species. In the present study these and other characters have been used to compare specimens from localities unknown to them. The results of this comparison are shown in Table 2.

Characters regarded by Lidicker and Marlow to demonstrate species differences are as follows:

(1) Tail length and brush length: Lidicker and Marlow consider the length of the caudal brush (pencil) to be one of the most diagnostic measurements in *Antechinomys*, their calculated mean for individuals of the nominate form (not including the Cedar Bay specimen) being 51.8 mm and their mean of the 'spenceri' form being 61 mm (observed range being 56 to 70). The only two specimens of Warburton Range *Antechinomys* ('spenceri' form) measured in the present study have a mean brush length of 54.3 mm with a range of 52.8–55.8. This almost certainly overlaps the range of the nominate form. Other isolated individuals and populations examined in the present study demonstrate considerable variation in brush length, although there is a tendency for absolutely larger brush lengths to occur in more inland animals. An exception is the animals from Lake Grace which, although certainly in a less central situation than the Warburton Range, have a mean brush length of 70.1 mm. When brush length is expressed as a proportion of total tail length, the mean of individual animals from the Warburton Range and Tobermoray is the same, 0.44. In fact all the means except that of Lake Grace animals, have comparable values, including that for the nominate form and animals from southern Queensland, considered by Lidicker and Marlow to represent the nominate form (the

latter 'mean' was determined using Lidicker and Marlow's figures for brush length and tail length). Evidently, despite apparent differences in absolute brush length, most *Antechinomys* have a reasonably constant proportion of their tail taken up by a brush.

(2) Hind foot length: From Lidicker and Marlow's figure 2, the mean standardized hind foot length of the typical form is 28.5 mm (not including the Cedar Bay specimen which is 26.2 mm). The same measurements given by them for the 'spenceri' form range from 30.0 to 31.6 mm. Foot measurements taken in this study from dry and alcohol specimens were standardized as suggested by Lidicker and Marlow (p. 213) and are shown in Table 2. The mean (27.7) given in the present study for the Lake Grace animals differs from that (30.0 mm) given by Lidicker and Marlow. The labels of WAM M2230 and M2368 both give '3.0' for hind foot measurements. Dry measurements (*su*) made on both specimens give 28.8 for WAM M2230 and 23.8 for WAM M2368. Standardizing these by adding 1.4 mm, the values are 30.2 and 25.2 mm and the mean, 27.7 mm. Evidently mean foot length of *Antechinomys* increases in central Australian localities, being smallest in peripheral, relatively less-arid areas such as Roper River, Lake Grace and New South Wales.

(3) M_{1-3} and M^{1-4} : The mean M_{1-3} length in *Antechinomys* shows only slight differences for populations referable to the 'spenceri' and nominate forms. Only the Cedar Bay individual stands out by being 0.3 mm smaller than any other specimen of *Antechinomys*. M^{1-4} is used by Lidicker and Marlow as a basis for comparison. The difference in mean values and observed ranges are similar to those of M^{1-3} except that the mean of animals from the Nullarbor sample is smaller than that of animals referable to the 'spenceri' form from central Western Australia. Mean M^{1-4} given by Lidicker and Marlow for the nominate form is 5.1 mm. This contrasts with the higher (5.4–5.9) mean values for populations they consider to represent the 'spenceri' form. Mean M^{1-4} value for the Tobermoray population is 5.1 mm. One Tobermoray male has a value of 5.7, which exceeds by 0.3 any specimen of the nominate form measured by Lidicker and Marlow.

(4) $C_1 - P_1$ space and $C_1 - P_1$ alveolar distance: Lidicker and Marlow conclude that the nominate form has a $C_1 - P_1$ space (presumably shortest distance between C_1 and P_1 crowns) of less than 0.2 mm, while the 'spenceri' form has a length of 0.2 to 0.5 mm. This character appears to be somewhat

variable in samples examined in the present study. The highest values occur in individuals from southwestern Queensland and the Warburton Range, but the individual means of all non-Queensland *Antechinomys* populations were below 0.2 mm. $C_1 - P_1$ alveolar distance (maximum distance between anterior edge of C_1 and posterior edge of P_1 alveoli) was measured in order to allow comparison with the large sample of Nullarbor specimens which, in most cases, lack C_1 . Means of specimens from the Warburton Range and Lake Grace are identical (2.38 mm). The only very different specimens are several from southwestern Queensland with high values (2.75 and 2.80 mm). The Nullarbor sample (37 individuals) had the lowest mean value (1.99 mm). These two measurements are of doubtful value. It is probable that even though all specimens measured were adult, the size of this feature will increase with age.

(5) Tympanic wing (or bulla) size, absolute and as a ratio: An examination of the distribution of absolute tympanic wing size indicates that means of animals from New South Wales, Cedar Bay, Roper River area, Tobermoray and Lake Grace are all relatively small. Means of animals from central Australia are high. There is also overlap in the observed ranges between central Australian and Tobermoray specimens. Alisphenoid tympanic wing (or bulla) width (BW, Table 2) is determined by subtracting the minimum distance (IBW, Table 1) between the left and right alisphenoid tympanic wings from the maximum distance (OBW, Table 1) between the left and right alisphenoid tympanic wings (the latter is measured from dorso-lateral points on the tympanic wing of the alisphenoid mesial to the glenoid fossa of the squamosal). BW is thus the composite width of both alisphenoid tympanic wings. The BW/zygomatic width (ZW, Tables 1–2) ratio is an estimate of the amount of cranial width represented by tympanic wing development. Specimens from the Warburton Range area have a very high mean, matched only by isolated animals from southwestern Queensland. Specimens from Lake Grace have a very low figure, even lower than the Cedar Bay specimen. In this regard, specimens from Roper River and Cedar Bay are similar, both having relatively small tympanic wings. About the same degree of similarity exists between Roper River and Tobermoray specimens as between the latter and specimens from central Western Australia, although the central specimens have the largest tympanic wing development. There appears to be a trend with larger tympanic wings occurring in progressively more arid areas.

(6) Cranial height: This character appears to vary in the same way as tympanic wing size and reflects the fact that cranial height, as described by Lidicker and Marlow (1970), involves maximum vertical height of the alisphenoid tympanic wings.

(7) Rostral width, length, and a relative ratio: Rostral width is shown by Lidicker and Marlow (their table 1) to be smaller in the nominate form, with no overlap in observed range between the 'spenceri' and the typical forms, except in the isolated Cedar Bay specimen. Examination here of larger and additional samples reveals a broad overlap between most populations of *Antechinomys*. Rostral length shows greater variation and even broader overlap in observed range between all populations. The ratio of RW/RL has also been examined. Two sorts of values are presented in Table 2. The first is the mean of the ratios for specimens examined in this study. The second is an approximated mean determined by using the means for rostral width and rostral length given by Lidicker and Marlow (their table 1). At least in the case of specimens from Warburton Range, the resultant figure is the same. In any case, differences for any given population are slight. In particular it should be noted that the 'mean' (0.35) of specimens referable to the nominate form is the same as that for specimens referable to the 'spenceri' form from the Warburton Range. This indicated that although slight differences occur in absolute measurements, proportions of the rostrum are clearly similar in both forms.

(8) Other characters: Most characters examined in this and Lidicker and Marlow's study show marked overlap in range in specimens referable to the 'spenceri' and nominate forms.

Of the characters used by Lidicker and Marlow to diagnose species of *Antechinomys*, nipple number alone seems not to overlap in the two forms, with the nominate form having eight to ten and the 'spenceri' form, four to six.

RECOGNIZABLE FORMS OF *Antechinomys laniger*

There seems little point in recognizing more than two (or possibly three if the Cedar Bay specimen is regarded as unique) forms of *A. laniger*. Use of the name 'spenceri' to distinguish the central Australian form is not to be interpreted as recognition here of its subspecific status because no attempt has been made to determine the statistical validity of the forms of *A. laniger* as subspecies.

The Nullarbor population has not been referred here to any particular form because material available for examination is incomplete. Lundelius

and Turnbull (1975) refer it to *spenceri* but note that the differences involved are slight and of dubious diagnostic value.

The nominate form (Plates 8–10, 12A–C, 13C–F) may be distinguished from the 'spenceri' form by its relatively smaller size, narrower palate, narrower skull, shorter caudal brush, shorter ears, shallower skull, smaller tympanic wings, and possession of eight nipples (this latter character has not been checked in all populations). Its range includes northern Victoria, New South Wales west of the Divide, south central Queensland, the Roper River Mission area and Tobermoray in the Northern Territory, the Lake Grace area of Western Australia, and the Cedar Bay in northeastern Queensland. The holotype of *Phascogale lanigera* Gould occurs within this range.

Because the nominate form is structurally ancestral and most similar to species of *Sminthopsis*, it is possible that only populations referable to the 'spenceri' form have markedly diverged from the ancestral stock. However, it is also possible that some populations referred here to the nominate form (such as those from Tobermoray) are derivatives of the 'spenceri' form which have secondarily come to resemble the nominate form by re-adapting to relatively less-arid areas.

The 'spenceri' form (Figs. 1–2, Plates 11, 12D–E, 13A–B) may be recognized by its relatively larger size, wider palate, wider skull, longer caudal brush, longer ears, deeper skull, larger bullae, and possession of six nipples. Jones (1923) gives a good description of this form which is supplemented by the description given by Lidicker and Marlow. The range of this form includes the southern Northern Territory, central Western Australia, northern South Australia, and southwestern Queensland. The holotype of *Antechinomys spenceri* Thomas evidently comes from Charlotte Waters, within this range.

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